A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida : Oligochaeta).

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Synopsis

Michaelsen (1921 & 1928) proposed a classification of earthworms based primarily on the structure and arrangement of genital systems. The classification gradually became a matter of controversy until eventually apart from megascolecoid species and members of the Lumbricidae, all other taxa were assigned to a heterogeneous Glossoscolecidae. Gates (1976*a*) recognized the systematic significance of common characters in the morphology of the ovaries and the process of shedding oocytes among members of the Lumbricidae and their undoubted allies which he employed to define the superfamily Lumbricoidea. These and other criteria are applied in a classification of the 16 families, 4 with 2 subfamilies, now forming the suborder Lumbricina with the recognition of five superfamilies. The present day distributions of the superfamilies are discussed in the context of palaeogeography: Criodriloidea and Lumbricoidea (Euramerica), Biwadriloidea (Pacifica, eastern Gondwana), Glossoscolecoidea (western Gondwana), Megascolecoidea (Gondwana).

Introduction

A biological classification is not static; it is transitory since a present day fauna represents a cross-section of evolutionary time and differs from both its antecedents and its descendents (Manton, 1977). Although aspects of this view of a classification are challengeable, the primary thesis is particularly apposite to those animal groups whose fossil histories are fragmentary or unknown. It introduces a dynamic concept into the formulation of affinities since, in many cases, change is inevitable but not solely because of animal evolution. Immediate reasons for modification are more likely to be due to a classification combining the totality of current knowledge of a group with contemporary zoological thought. Hence, frequent alteration is probable while new information and ideas continue to be advanced. Change was common during the nineteenth century as the numerous classifications proposed for the Oligochaeta provide testimony (Beddard, 1895). Beddard himself recognized three 'Groups': Aphaneura, Microdrili and Megadrili. The last, Megadrili, consisted of the true earthworms and their aquatic representatives and is equivalent to the suborder Lumbricina. Contemporary knowledge led Beddard to recognize only the following higher groups in his Megadrili : the single families Geoscolecidae (= Glossoscolecidae), Eudrilidae,

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Lumbricidae and the superfamily Megascolecidae (sic) containing the families Perichaetidae, Cryptodrilidae and Acanthodrilidae of which the Perichaetidae contained perichaetine Megascolecidae *sensu* Gates (1959) and the last two comprised highly heterogeneous assemblages of megascolecoid genera. Since then many new taxa have been described and 16 families, four each with two subfamilies, are now recognized within the suborder (see below).

During the present century, the scientific contributions made by Professor Wilhelm Michaelsen between 1885 and 1938 have, justly, dominated oligochaetology and have fundamentally influenced its theory (Klatt, 1938). Michaelsen took the first steps towards constructing a comprehensive classification of the Oligochaeta in 1900 when he recognized new family groups some with subfamilies. The characters employed to delineate the basic units, the genera, and the families themselves were derived predominantly from the genital systems, especially the male terminalia. When he formally presented a structured classification in 1921 (modified slightly in 1928), it became clear that he did not regard these characters as markers (signifying a summation of other, somatic characters) but as being phylogenetically significant *per se*. Thus he engendered the belief that the genital systems are evolutionarily conservative while somatic characters are more liable to modification. This viewpoint subsequently had a profound influence on other authors, notably Stephenson (1930) and Yamaguchi (1953). Nevertheless Stephenson was uncertain about the higher systematics and dispensed with groups above the level of family in his great monograph.

Gradually information accumulated from intensive morphological studies, especially on the Lumbricina, and contributed towards a growing awareness that the 'classical' system of Michaelsen was no longer tenable and could not be regarded as inviolable. Moreover, against modern theories of speciation and evolution, many of Michaelsen's premises could be seen to be outmoded. A naivité of hypothesis was also widespread with most groups, genera or occasionally species, believed to be derived from extant groups; that is, ancestor and descendent were sympatric contemporaries. (Only infrequently were hypothetical common ancestors postulated to help explain present day relationships.) Generally there seemed to be a lack of awareness of knowledge derived from other animal groups, particularly those with rich fossil records. Consequently there was a failure to acknowledge that events in other groups could conceivably be paralleled in the Oligochaeta. Particularly the possibility that in the past more species and groups may have emerged and become extinct than survive to form the present day fauna. (A penetrating critique of the 'classical' system was presented by Gates (1972) in which he enumerated its many fallacies and others which have been derived from it.)

Most early difficulties were encountered in defining genera and consequently classifying them into families and the higher categories forming the suborder Lumbricina. The genera contained within the Megascolecoidea have always been accepted as forming a separate entity although apart from the Eudrilidae, there is still no general agreement on the number of families represented or the characters which should be employed to recognize them (Sims, 1966; Jamieson, 1971*b*). As for the non-megascolecoid genera, eventually they became to be assigned either as a series of families in a single superfamily (Yamguchi, 1953) or to the Lumbricidae *s.s.* (species with dorsal pores, pre-clitellar male pores, intestinal gizzards and lacking oesophageal gizzards) and all others to a highly structured Glossoscolecidae containing subfamilies and tribes (Jamieson, 1971*a*). Both treatments obscured the interrelationships of the included members and prevented a constructive discussion of the biogeography of the suborder. The problems encountered in accommodating new incontravertible lumbricoid genera led Gates to seek different criteria to obtain a new basis for a classification. Eventually he concluded that the morphology of the ovaries and the process of shedding oocytes provided attributes which could be employed to define the superfamily Lumbricoidea resulting in the formation of a seemingly homogeneous assemblage of families (Gates, 1976*a*).

Recently the debate on the classification of the Lumbricina was thrown open wider when Jamieson (1978) reported on a computer based investigation of the opisthoporous Oligochaeta. The principles of Hennig for deducing phylogeny were adapted for computer study and the attributes were analysed in an attempt to obtain a phylogenetic classification. As is often the case with taximetric studies, the results tended to reveal some evidence of primary categories but indications of secondary or lower categories were inconclusive. Nevertheless Jamieson proposed a classification of the Haplotaxida which apart from the inclusion of the Moniligastridae (accommodated in a separate suborder), is largely familiar but the compositions of the superfamilies forming the suborder Lumbricina although valid according to the methods employed, were seemingly artificial since their common characters were often adaptive (e.g. Almoidea = Almidae + Criodrilidae + Lutodrilidae); not surprisingly the distributional implications were incompatible with zoogeographical knowledge.

These problems however do not arise if the criteria recognized by Gates for defining the Lumbricoidea, the morphology of the ovaries and the budding of the oocytes, are applied together with other characters to all members of the Lumbricina. By utilizing these characters, superfamilies may be recognized which when polytypic, contain morphologically homogeneous assemblages which have common zoogeographical provenances. The ovarian characters recognized could be phylogenetically significant as they are seemingly non-adaptive, certainly it is difficult to suggest any selective agencies likely to have influenced their evolution.

Classification

The classification of the superfamilies proposed below is based on the ovarian characters first recognized by Gates (1976*a*) as useful for defining the Lumbricoidea. The structures regarded as systematically significant are seldom detailed by authors since they can be observed only by careful dissection in well-preserved material. During the preparation of this present work, it was impracticable to examine material representative of all of the 3000 or so species forming the Lumbricina, so only sample species were dissected. In these circumstances the classification can be no more than tentative and some characters may, in time, be found to be variable in their expression. However, when the validities of the component groups are not doubted, variation in a key character need not invalidate the classification; instead only the weighting and definition of the taxonomic criteria may need re-assessment and modification*.

Each family and, when recognized, subfamily is briefly defined to assist in identification. Many of the characters listed are not individually diagnostic but when present in varying combinations with other attributes, permit groups to be recognized. A few characters, some possibly of phylogenetic significance, are not included especially those derived from the vascular and excretory systems. These details are omitted due to the paucity of reliable information about their expressions in many species of the larger families.

Meanwhile parts of the classification are likely to remain controversial until the significance of a few characters has been more rigorously investigated or additional structures are recognized as being taxonomically important. For example, many components of the Megascolecoidea currently defy classification into groups which receive universal accep-

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*Gates (1968) described the genus and species *Thamnodriloides yunkeri* (family Glossoscolecidae, superfamily Glossoscolecoidea) on a single aberrant specimen with oocytes forming numerous egg-strings, a character diagnostic of the superfamily Megascolecoidea. Variation in this character has not been studied so the significance of the observation is unknown. However, in some Glossoscolecoidea, the ovaries tend not only to be lobate but occasionally have filaments which in preserved specimens may be interpreted as egg-strings. Gates (*personal communication*) warned of variations in the form of the ovary and disposition of the oocytes in preserved specimens, for example in species where the oocytes are normally shed individually, on preservation they may form clumps which can be interpreted as strings. Like other attributes, the characters of the ovaries and the oocytes should be assessed on their expressions in series of specimens and not in individuals. In the case of *Thamnodriloides yunkeri*, the report of an exception in a single, aberrant specimen should not cause the system to be rejected since other characters present permit the species to be classified (fan-shaped ovaries, subneural vessel free of the nerve cord, the presence of a supra-oesophageal blood vessel and extra-mural calciferous glands and the absence of prostatic glands associated with the male pores).

tance. In this case, a pragmatic solution is adopted which although not entirely incompatible with available information, provides working groups composed of morphological grades which may not necessarily be phylogenetic assemblages.

Key to the families of the suborder LUMBRICINA

1	Prostatic glands present (discharging through or near male pores or on segments adjacent to the male pores) or 'prostate'-like bursae discharging through male pores	2
	Prostatic glands absent ('prostate'-like glands, when present, not associated with the male pores)	9
2	Male pores anterior to or on segment *xvi*	3
	Male pores posterior to segment *xvi*	5
3	Male pores on segment *xiii* (lateral line present, aquatic, Japan)	**BIWADRILIDAE**
	Male pores on segments *xv* or *xvi* (lateral line absent)	4
4	Body quadrangular (male pores on porophores, aquatic Europe)	**CRIODRILIDAE**
	Body cylindrical (male pores in copulatory pouches, terrestrial Madagascar)	**KYNOTIDAE**
5(2)	Spermathecae present in pre-testicular segments	6
	Spermathecae absent from pre-testicular segments (received sperm contained in coelomic sacs associated or communicating with the ovisacs and oviducts) .	**EUDRILIDAE**
6	Prostatic glands racemose without central duct	**MEGASCOLECIDAE**
	Prostatic glands tubular with central duct	7
7	Meronephric	**OCTOCHAETIDAE**
	Holonephric	8
8	Last hearts or homoetic equivalent in segment *xi*	**OCNERODRILIDAE**
	Last hearts posterior to segment *xi*.	**ACANTHODRILIDAE**
9(1)	Oesophageal gizzard(s) or gizzard-like dilation(s) present in the pre-testicular segments	10
	Oesophageal gizzard(s) or gizzard-like dilation(s) absent from the pre-testicular segments	14
10	Extra-mural calciferous glands present	11
	Extra-mural calciferous glands absent	12
11	Gizzard in segment *vi* (supra-oesophageal blood vessel present)	**GLOSSOSCOLECIDAE**
	Gizzard in segment *vii* (supra-oesophageal blood vessel absent).	**MICROCHAETIDAE**
12(10)	Body quadrangular in cross-section, at least in the post-clitellar region (supra-oesophageal blood vessel present)	**ALMIDAE**
	Body cylindrical (supra-oesophageal blood vessel absent).	13
13	Male pores paired on segment *xv* (2 or 3 gizzards, each restricted to a single segment)	**HORMOGASTRIDAE**
	Male pores paired on segment *xxii* (1 gizzard restricted to a single segment, or, 2 gizzards each occupying two segments)	**AILOSCOLECIDAE**
14(9)	Testes 2 pairs in segments *x* and *xi* (intestinal gizzards, when present, in some or all of segments *xvii*-*xx*)	15

Testes 10 pairs in segments *xii-xxi* (intestinal dilation in segments *xxi-xxiv*) . . . . **LUTODRILIDAE**

15 Intestinal gizzards present (intra-mural calciferous glands present) . **LUMBRICIDAE**
Intestinal gizzards absent (calciferous glands absent) . **SPARGANOPHILIDAE**

Suborder **LUMBRICINA**

Earthworms and their aquatic representatives: clitellum formed from multiple layers of cells; testes usually 1 or 2 pairs in *x* and/or *xi* (exceptionally numerous: *Agastrodrilus*, family Octochaetidae, 9 pairs and *Lutodrilus*, family Lutodrilidae, 10 pairs) when there are 2 pairs of testes, the two vasa deferentia of each side usually unite; male pores 1 pair, rarely 2 pairs, at least two segments behind the posterior testes; ovaries commonly 1 pair in *xiii* (*xiv* and *xx* in *Agastrodrilus, xxiii* in *Lutodrilus*), oocytes small, not yolky; female pores in *xiv* (*xv* and *xxi* in *Agastrodrilus* and *xxiv* in *Lutodrilus*).

DISTRIBUTION. World wide, except Antarctica.

Superfamily **CRIODRILOIDEA**

Fresh and brackish water worms: lateral line absent; ovaries small, flattened, pear to paddle-shaped, oocytes shed individually, not forming egg-strings; calciferous glands absent; supra-oesophageal vessel absent; subneural vessel adherent to the nerve cord; hearts lateral.
Single family.

DISTRIBUTION. Southwestern palaearctic.

Family **CRIODRILIDAE** Vejdovsky, 1884.

Fresh and brackish water worms: body quadrangular in cross-section; dorsal pores absent; clitellum annular, extensive, indistinctly delimited anteriorly and posteriorly (*xiv, xv*) *xvi–xxxxv* (*xxxxvi*), tubercula pubertatis absent; male pores paired *xv* on porophores; spermathecal pores absent (tubular to hornshaped spermatophores usually present on the body wall near *xiii*); gizzard? rudimentary (oesophageal wall thickened *v–vii*), intestine thickened anteriorly *xv–xx* (*xxi*); paired hemispherical bursae or 'prostatic glands' *xv*; spermathecae absent; meganephridial.
Single genus with two(?) species.

DISTRIBUTION. France, Germany, Italy, Yugoslavia, Hungary, Poland, southern U.S.S.R., Syria and Israel; introduced into the U.S.A. (plant pots, Baltimore).

Superfamily **LUMBRICOIDEA**

Earthworms some freshwater: lateral line absent exceptionally rudimentary (Sparganophilidae); ovaries small, discoidal with the oocytes forming a single egg-string; supra-oesophageal vessel absent; subneural vessel, when present, adherent to the nerve cord; hearts lateral.
Five families.

DISTRIBUTION. Holarctic, some species introduced into other regions

Family **SPARGANOPHILIDAE** Michaelsen, 1928

Freshwater worms: body cylindrical but capable of forming a dorsal groove; lateral line doubtfully present; dorsal pores sometimes present anteriorly or absent throughout; clitellum saddle-shaped (*Sparganophilus tamesis* and *pearsei*) or annular (*S. smithi*), (*xiv*)

xv–xxv (*xxviii*), paired tubercula pubertatis present, usually ridge-like but may be divided intersegmentally to form a series of pads; male pores paired, inconspicuous, 18/19 or *xix*, intraclitellar; spermathecal pores paired or multiple, inconspicuous (5/6) 6/7/9; gizzards and calciferous glands absent; prostate-like glands present, *not* associated with the male pores, possibly up to 14 pairs but commonly 4 or less in *xxii–xxvi;* spermathecae one to four pairs per thecal segment, adiverticulate; meganephridial.
Single genus and 3 species.

DISTRIBUTION. North and Central America (Ontario, Michigan, North Carolina, California, Guatemala, Mexico); introduced into Britain and France.

Family **AILOSCOLECIDAE** Bouché, 1969

(syn. Komarekionidae Gates, 1974)*

Earthworms: body cylindrical, dorsal pores absent; clitellum partly annular (*Ailscolex*), otherwise saddle-shaped, *xiv–xxiv*; tubercula pubertatis paired as continuous bands throughout most of the saddle-shaped region of the clitellum; male pores paired, inconspicuous *xxii*; spermathecal pores 6/7/8/9 (*Komarekiona*) and 8/9/10 (*Ailoscolex*); oesophageal gizzard(s) present, single in *vi* (*Komarekiona*) or 2 gizzards the first in *vi, vii* and the second in *viii, ix* (*Ailoscolex*), intestinal gizzards absent; calciferous glands absent; tubular, prostate-like glands associated with the tubercula pubertatis and (*Komarekiona*) additionally associated with the ventral setae in some segments *vii–xxvi*; spermathecae adiverticulate; meganephridial.
Two monotypic genera.

DISTRIBUTION. *Ailoscolex* southwestern France (central Pyrenees); *Komarekiona* southeastern United States (North Carolina, Tennessee and Indiana).

Family **HORMOGASTRIDAE** Michaelsen, 1900.

Earthworms: usually large, body cylindrical; dorsal pores absent; lateral setae more closely paired than ventral setae; clitellum saddle-shaped (*xiii*) *xiv–xxiv* (*xxxii*), tubercula pubertatis paired, ridge-like (*xxvii*) *xix–xxiv* (*xxix*); male pores *xv* by 15/16, preclitellar; spermathecal pores inconspicuous, paired or multiple 9/10/11/12/13/14/(15); 2 or 3 oesophageal gizzards *vi–viii*; single intestinal gizzard rudimentary *xv, xvi* (*xviii*); calciferous glands ?absent, prostatic glands absent; spermathecae adivertculate; meganephridial.
Two doubtfully distinct subfamilies.

DISTRIBUTION. Western Mediterranean countries.

Subfamily **HORMOGASTRINAE** Michaelsen, 1900.

Tubercula pubertatis (*xxvii*) *xix–xxiii* (*xxix*); spermathecal pores paired or multiple, 9/10/11/12/13/14/(15); 3 oesophageal gizzards.
2 genera containing 3 species.

DISTRIBUTION. Sicily, Italy, Sardinia, Corsica, southern France and Spain; one species (introduced?) Algeria and Tunisia.

Subfamily **VIGNYSINAE** Bouché, 1970.

Tubercula pubertatis *xxi–xxiv*; spermathecal pores paired, 9/10/11; 2 oesophageal gizzards, anterior half of *vi* and by 6/7.

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*The similarities between *Ailoscolex* Bouché, 1969 and *Komarekiona* Gates, 1974 have not been recognized previously, possibly because of a printing error in Bouché's monograph (1972). In this work, the diagnosis of the family Ailoscolecidae included the statement "Glande de Morren présente" (p. 197), whereas in the account of the anatomy of *A. lacteospumosus* there is the conflicting statement "Glande de Morren absente" (p. 199). The absence of calciferous glands however, was previously established in the original descriptions of the family and species (Bouché, 1969 : 526, 529 & 530).

Single genus and species.

DISTRIBUTION. Southern France (hinterland of Montpelier)

Family **LUMBRICIDAE** Rafinesque-Schmaltz, 1815

Earthworms: body mainly cylindrical sometimes with the posterior region depressed or infrequently body quadrangular, octagonal or trapezoidal in cross section; dorsal pores usually present, exceptionally (Diporodrilinae) replaced by paired, intersegmental, dorsolateral coelomic pores; clitellum usually saddle-shaped occupying 4–32 segments between *xvii* and *lii*, tubercula pubertatis present, band-like or papillose; male pores paired *xv*, rarely *xiii* or *xiv*, preclitellar; spermathecal pores paired in 2–8 furrows between 5/6 to 19/20 located anywhere between setal line *a* and near the mid-dorsal line (commonly 2 pairs present between setal lines *cd* in furrows 9/10/11); oesophageal gizzard absent; intestinal gizzard present in 1 or 2 segments in *xvii–xx*, preceded by a crop in a single segment in *xv–xvii*; calciferous glands intra-mural in some or all of (*ix*) *x–xv*; prostatic glands absent; spermathecae paired, adiverticulate, either interparietal or extending freely into the coelom; meganephridial.
Two subfamilies.

DISTRIBUTION. Palaearctic region and eastern North America; some species introduced into other regions.

Subfamily **LUMBRICINAE** Rafinesque-Schmaltz, 1815.
Single dorsal pores present; intestinal gizzard confined to a single segment.
20 or more genera of disputed validities containing some 300 species.

DISTRIBUTION. Palaearctic region (poorly represented in Asia) and a few species in areas of North America to the east of the Midwest lands once submerged beneath Cretaceous seas; about 10 mainly edaphophagous species inhabiting temporary burrows, introduced into other regions of the world.

Subfamily **DIPORODRILINAE** Bouché, 1970.
Single dorsal pores absent, replaced by paired, intersegmental coelomic pores; intestinal gizzard occupying two segments.
Single genus with 2 species.

DISTRIBUTION. Corsica.

Family **LUTODRILIDAE** McMahan, 1976.

Earthworms of river-side or river muds: body quadrangular; dorsal pores absent; clitellum annular, occupying 35–51 segments (*xx*) *xxv–lxi* (*lxxi*), tubercula pubertatis paired, extending throughout most of the clitellar region, aliform; male pores paired *xxxii*, intraclitellar; female pores paired *xxiv*; spermathecal pores multiple 15/16–25/26; oesophageal gizzard absent; intestinal dilation present *xxi–xxiv*; calciferous glands absent; testes 10 pairs, *xii–xxi*; prostatic glands absent; ovaries paired in *xxiii*; spermathecae adiverticulate, multiple, interparietal; meganephridial.
Single genus and species

DISTRIBUTION. Southeastern United States (southeastern Louisiana between the Mississippi and Pearl rivers).

Superfamily **BIWADRILOIDEA**

Freshwater worms: lateral line present between the dorsal and ventral setal couples; ovaries small, lobate (conical in young individuals), oocytes shed (?) individually, not forming

strings; calciferous glands absent; supra-oesophageal vessel present; subneural vessel absent; hearts lateral.
Single family.

DISTRIBUTION. Japan.

Family **BIWADRILIDAE** Jamieson, 1971*a*

Freshwater worms: body cylindrical (swollen laterally in the region of the male pores); dorsal pores absent; clitellum annular, extensive (*xiv*) *xv–xxxi* (*xxxiv*), tubercula pubertatis absent, paired quadrangular porophores carry the male pores on *xiii*; spermathecal pores absent (conical to thecal-shaped spermatophores usually present in pairs near the male pores particularly on the dorsal and dorso-lateral body walls); gizzards absent; prostatic glands lobular *xiii*, in addition paired cylindrical setal glands discharge by the genital setae ventrally to the prostatic ducts; spermathecae absent; meganephridial.
Single genus and species.

DISTRIBUTION. Japan in streams, rice paddies and lakes (Lake Biwa, 60 m).

Superfamily **GLOSSOSCOLECOIDEA**

Earthworms some freshwater exceptionally littoral: lateral line absent; ovaries large, elongately band or ribbon-shaped, tending to become lobate with several digitiform processes, oocytes not forming egg-strings; calciferous glands, when present, extra-mural; supra-oesophageal vessel usually present; subneural vessel, when present, free of the nerve cord, adherent to the parietes; some hearts latero-oesophageal.
Four families.

DISTRIBUTION. America, Africa and Madagascar, southern India and southeastern Asia to western Indo-Australasian archipelago.

Family **KYNOTIDAE** Jamieson, 1971*a*

Earthworms: body cylindrical; dorsal pores absent; clitellum annular or saddle-shaped *xviii–xxxxvii*, tubercula pubertatis absent; male pores paired *xvi*, rarely *xv*, within copulatory pouches which when everted form clasper-like 'appendages', preclitellar; spermathecal pores inconspicuous, multiple 13/14/15/16; oesophageal gizzard *v*; intestinal gizzard(s) absent; calciferous glands absent; supra-oesophageal vessel present; tubular prostate-like setal glands associated with the copulatory pouches; spermathecae adiverticulate, multiple; meganephridial.
Single genus containing 12 or so species.

DISTRIBUTION. Madagascar (primary forest).

Family **MICROCHAETIDAE** Michaelsen, 1900.

Earthworms: body cylindrical; dorsal pores absent; clitellum saddle-shaped extending 20 or so segments *ix–xxxiv*, tubercula pubertatis present, ridge-like or papillose; male pores paired behind *xvi*; intraclitellar; spermathecal pores sometimes absent otherwise inconspicuous, usually multiple, occasionally paired, in some or all 10/11–15/16; oesophageal gizzard *vii*; intestinal gizzard(s) absent; calciferous glands single pair near 9/10; subneural and supra-oesophageal vessels absent; prostatic glands absent, setal glands associated with the genital setae (copulatory sacs absent); spermathecae adiverticulate, sometimes serpentine; usually meganephridial with additional numerous coiled loops in the anterior segments which are often enteronephric, rarely (*Tritogenia*) 2 pairs of meronephridia in each segment.
Three genera containing 33 species.

Distribution. Republic of South Africa (primary grasslands).

Family **GLOSSOSCOLECIDAE** Michaelsen, 1900.

Earthworms exceptionally (*Pontoscolex*) on beaches perhaps littoral: body cylindrical; dorsal pores seldom present; four pairs of setae in each segment occasionally with the setal couples alternatively closely and widely paired in successive segments (e.g. *Pontoscolex*), rarely setae numerous (*Periscolex*); clitellum saddle-shaped occupying up to 12 segments beginning near *xiv,* tubercula pubertatis present; male pores inconspicuous sometimes within copulatory pouches, usually intraclitellar rarely post clitellar (*Opisthodrilus*), exceptionally 2 pairs (*Eudevoscolex*); spermathecal pores inconspicuous, usually paired, seldom multiple, mainly pretesticular occasionally including the testicular segments; oesophageal gizzard in *vi*; intestinal dilation in the region of *xvi*; calciferous glands extra-mural, 1–8 pairs between *vii–xiv*; supra-oesophageal vessel present; prostatic glands absent; spermathecae adiverticulate either interparietal or extending freely into the coelom; meganephridial.
About 25 genera containing nearly 200 species.

Distribution. Central America including many Caribbean islands and tropical South America (wide range of habitats, predominantly forest soils), *Pontoscolex* now circum-tropical on or near beaches.

Family **ALMIDAE** Duboscq, 1902.

Freshwater worms often in riverside muds: body quadrangular in cross-section, at least behind the clitellum, setal pairs commonly located near the angles; dorsal groove commonly present; dorsal pores absent; clitellum annular, variable length and location (*Callidrilus* 19–29 segments beginning in or behind *xii, Drilocrius* and *Glyphidrilocrius* 22–30 or so segments beginning near male pore *Glyphidrilus* 17–35 segments beginning in or near *xlii*; *Alma* 20–69 segments between *xxxv–ccvc*); tubercula pubertatis ridge-like (*Callidrilus*), aliform (*Glyphidrilus* and *Glyphidrilocrius*) or absent (*Alma* and *Drilocrius*); male pores inconspicuous, a single pair between *xv–xxx,* preclitellar or intraclitellar, sometimes near base of paired genital lobes (*Drilocrius*) or distally on paired ribbon-like claspers (*Alma*); spermathecal pores inconspicuous, multiple, intersegmental between *vii* to about *cc,* usually post-testicualr, especially numerous near setal lines; oesophageal 'gizzards' present as 1–3 dilations in *v–ix*; intestinal gizzards absent; calciferous glands absent; supra-oesophageal vessel present; 'prostatic-like' glands rarely present (*Callidrilus*); spermathecae adiverticulate partly or wholly interparietal; megnephridial.
Six genera (including *Areco* Righi, Ayres & Bittencourt, 1978) containing nearly 40 species.

Distribution. Tropical America, Africa, peninsular India, Burma, Malaysia and Indonesia eastwards to Sulawesi (aquatic or riverside muds).

Superfamily **MEGASCOLECOIDEA**

Earthworms, some associated with freshwater or exceptionally littoral: lateral line absent; ovaries large, fan to rosette-shaped with the oocytes forming several egg strings; calciferous glands extramural; supra-oesophageal vessel often present; subneural vessel, when present, free of the nerve cord and attached to the parietes. Some hearts latero-oesophageal.
Five families.

Distribution. Southern hemisphere (not Antarctica) and tropics also middle and western North America, eastern U.S.S.R., Japan, Korea and southern China; a few species of most families introduced into other regions.

Family **OCNERODRILIDAE** Beddard, 1891.

Earthworms often associated with freshwater: body cylindrical; dorsal pores seldom present; clitellum annular or saddle-shaped usually occupying up to 7 segments between *xii–xviii* exceptionally (*Nematogenia*) 13 segments in length extending backwards to *xxvi,* tubercula pubertatis absent but genital papillae and/or porophores common; male pores paired *xvii* or *xviii,* rarely *xix* or *xx,* intraclitellar or commonly by the posterior margin of the clitellum; prostatic pores 1–3 pairs between *xvi–xxi*; spermathecal pores pretesticular; 1 or 2 oesophageal gizzards; intestinal gizzards absent; calciferous glands *ix* and *x* (Ocnerodrilinae); supra-oesophageal vessel present; prostatic glands tubular with central canal, 1–3 pairs; spermathecae seldom diverticulate; meganephridial.
Two subfamilies.

Distribution. Most of tropical America, both tropical and southern Africa, some Indian Ocean Islands, southern India and nearby areas; a few species introduced elsewhere, mainly tropical areas.

Subfamily **OCNERODRILINAE** Beddard, 1891.

Extra-mural calciferous glands present.
Twenty genera.

Distribution. Western North America from the Tropic of Cancer southwards through Central America and some Caribbean islands into South America to near the Tropic of Capricorn, throughout Africa from the Nile Valley and south of the Sahara into Madagascar and the Seychelles.

Subfamily **MALABARIINAE** Gates, 1966.

Calciferous glands absent.
Three genera.

Distribution. Peninsular India some species spreading into the Himalayan foothills and Burma.

Family **MEGASCOLECIDAE** Rosa, 1891.

Earthworms: body cylindrical; dorsal pores present; setae commonly four pairs on each segment sometimes numerous; clitellum annular or saddle-shaped usually occupying up to 7 segments between *xii–xviii,* tubercula pubertatis absent but genital marking and/or porophores common; male pores paired commonly on *xviii* (*xvii Nelloscolex* and *Tonoscolex,* rarely *xix* or *xx* in a few *Pheretima* s.l. spp.) immediately postclitellar; prostatic pores rare, usually prostatic ducts discharge through male pores, when present located on the same segment as the male pores (*Plutellus*) or more posteriorly (*Nelloscolex* and *Tonoscolex*); spermathecal pores paired or multiple, pretesticular; usually 1–3 oesophageal gizzards; intestinal gizzards rare (*Pleinogaster*), intestinal caeca sometimes present; calciferous glands often present; supra-oesophageal vessel(s) present; prostatic glands racemose in structure of mesoblastic origin without central duct, paired commonly in *xviii*; spermathecae usually diverticulate, paired or numerous; meganephridial or meronephridial.
About 25 genera containing over 1000 species.

Distribution. Eastern U.S.S.R., Japan, Korea, southern China to Australasia; some species (especially of the genus *Amynthas*) introduced into other regions.

Family **ACANTHODRILIDAE** Claus, 1880.

Earthworms seldom freshwater, exceptionally on beaches or littoral: body cylindrical; dorsal

pores present; setae commonly 4 pairs on each segment, seldom 5 or 6 pairs, exceptionally numerous; clitellum annular or saddle-shaped frequently occupying up to 6 or 7 segments between *xii–xviii,* tubercula pubertatis absent but genital markings and/or porophores common; male pores usually paired on *xviii* with paired prostatic pores on both *xvii* and *xix,* or, paired on *xvii* or *xix* with a single pair of prostatic pores on the same segment, prostatic pores rarely more posteriorly, male pores mainly by the posterior margin of the clitellum or intraclitellar; usually 1–3 oesophageal gizzards occasionally rudimentary or absent; intestinal gizzards absent; calciferous glands common; supra-oesophageal vessel often present; prostatic glands tubular in structure of ectodermal origin with central canal, 1 or 2 pairs in *xvii* and/or *xix*; spermathecae usually diverticulate; meganephridial.
Over 20 genera.

Distribution. Americas, tropical and southern Africa,? southeastern Asia, Australasia, islands of the Southern Ocean.

Family **OCTOCHAETIDAE** Michaelsen, 1900.

Earthworms: body cylindrical; dorsal pores usually present; setae 4 pairs on each segment; clitellum annular or saddle-shaped frequently occupying 6–7 segments between *xii–xviii* seldom more extensive, exceptionally (*Agastrodrilus*) occupying about 30 segments; tubercula pubertatis absent but genital papillae and/or porophores common; male pores usually paired on *xviii* with paired prostatic pores on both *xvii* and *xix,* or, paired on *xvii, xviii* or *xix* with a single pair of prostatic pores on the same segment or confluent, exceptionally (*Hoplochaetella*) 2 pairs of male pores each associated with the prostatic pores on *xvii* and *xix,* or, 9 pairs (*Agastrodrilus*), male pores mainly situated by the posterior margin of the clitellum or intraclitellar; spermathecal pores pretesticular; usually 1–3 oesophageal gizzards sometimes rudimentary or absent; intestinal gizzards absent, intestinal caeca rare (*Millsonia*); calciferous glands common; supra-oesophageal vessel common; prostatic glands tubular in structure of ectodermal origin with central canal, paired in both *xvii* and *xix* or a single pair in *xvii, xviii* or *xix*; meronephridial.
Nearly 30 genera.

Distribution. Temperate species: Australasia. Tropical species: tropical America and Africa, peninsular India and into Burma; *Dichogaster* spp. introduced into other regions.

Family **EUDRILIDAE** Claus, 1880.

Earthworms: body cylindrical; dorsal pores absent; setae 4 pairs on each segment, the dorsal pairs frequently closer together than the ventral pairs; clitellum annular or saddle-shaped, frequently occupying up to 6–7 segments between *xii–xviii,* tubercula pubertatis absent but genital papillae and/or porophores common; male pore(s) single or paired on *xvii* or in 17/18 confluent with the prostatic pore(s), located principally by the posterior margin of the clitellum; 'spermathecal' pore(s) single or paired rarely pretesticular, usually post-testicular and sometimes confluent with the female pores, exceptionally behind the male pore(s); 1 oesophageal gizzard commonly in *v,* rarely reduced or absent; intestinal gizzards rare (invariably present when oesophageal gizzard reduced or absent); intestinal caeca absent; calciferous glands present; supra-oesophageal vessel present; prostatic glands tubular, single pair, commonly elongately ovoid, modified as 'euprostates', sometimes long and slender; spermathecae either modified and associated with the ovaries or absent and replaced by a 'spermathecal' system derived from mesoblastic tissue, the 'spermathecal' system extends from the 'spermathecal' pore(s) to the ovarian segment where it is confluent with the oviducts, occasionally continuing more posteriorly as a blind coelomic sac; meganephridial.
Two subfamilies containing some 500 species.

Distribution. Tropical Africa south of the Sahara; a species of *Eudrilus* has been introduced into other regions.

Subfamily **PAREUDRILINAE** Beddard, 1894.
Calciferous glands unpaired suboesophageal sacs; testes free.
About 15 genera.

DISTRIBUTION. Tropical Africa, mostly in eastern areas.

Subfamily **EUDRILINAE** Claus, 1880.
Calciferous glands unpaired suboesophageal sacs in *ix–xi* or *xi–xii* and a single pair of lamellate glands in *xii* or *xiii*; each testis enclosed in a 'sperm reservoir' formed from the ental end of the associated vas deferens which is confluent with the seminal vesicle in the succeeding segment.
About 30 genera.

DISTRIBUTION. Tropical Africa, mostly in western areas.

Systematic discussion

Criodriloidea. The ovaries of the single(?) species forming this superfamily are not well described but they are known to be small while the oocytes are shed individually and do not form egg-strings. The same characters are shared with the Biwadriloidea with which there is a further resemblance in the presence of two cerebral ganglia situated anteriorly in segments *i* and *ii* but the latter condition is possibly only the retention of the primitive state. (There are additional similarities with the Glossoscolecoidea but they are mainly in negative characters.) Authors have commented on the similarities between the Criodrilidae and the Lumbricidae: thickening of the musculature at the anterior end of the intestine, copulatory sacs at the ends of the sperm ducts, male pores occurring on porophores on segment *xv*, presence of spermatophores (structures common in the megascolecoid genus *Polytreutus*, family Eudrilidae), absence of a supra-oesophageal blood vessel and the subneural blood vessel adhering to the ventral nerve cord (for a fuller account and discussion, *see* Jamieson, 1971*a*). (Additional morphological resemblances with other groups, e.g. quadrangular body section, are seemingly adaptations to an aquatic environment and have little place in this present discussion.) However, if phylogenetic importance is attached to the association of the subneural blood vessel with the ventral nerve cord and to the absence of a supra-oesophageal blood vessel, it may be concluded that the Criodriloidea and Lumbricoidea are derived from a common ancestor with the less highly organized Criodriloidea retaining several primitive characters.

Lumbricoidea. The characters of the ovary and formation of a single string of oocytes are the primary features distinguishing this superfamily from the closely allied Criodriloidea while for separation from the Glossoscolecoidea and Megascolecoidea can be added the association of the subneural blood vessel with the ventral nerve cord and the negative features, the absence of both a supra-oesophageal blood vessel and extra-mural calciferous glands. Among the Lumbricoidea, the monotypic Lutodrilidae is unique in possessing paired testes in numerous successive segments. This multiplicity of testes segments should not be regarded as a primitive condition retained from some archaic ancestor but more simply seen as an aberrant specialization (a view which is supported by the unusual location of the ovaries in segment *xxiii*, another aberrancy). Members of the family Sparganophilidae possess features consistent with an aquatic mode of life, the rudiments of a lateral line and the absence of gizzards and calciferous glands, yet the body has not acquired a quadrangular cross-section which it has in the aquatic *Lutodrilus* and *Eiseniella*. The constituent families are recognized mainly on a few common characters which are expressed in varying combinations, a situation frequently encountered among allied taxa. The inter-relationships of the members of the superfamily are obscure. Isolation during the Quaternary glacial epochs may have provided conditions favouring change but in view of the wide range of the

Lumbricidae, it seems more likely that the families emerged long before those events (*see below* Discussion). Presumably the small families are themselves relicts of larger, possibly more diverse, wider ranging groups.

Biwadriloidea. Gates (1976*a*) placed the family Biwadrilidae in the superfamily Lumbricoidea on the similarities between the morphology of the ovary of a figured young individual of *Biwadrilus bathybates* (Stephenson, 1917) and his own observations on the immature ovary in the lumbricoid *Lutodrilus multivesiculatus* McMahan, 1976 (family Lutodrilidae). He did so only tentatively because details of budding oocytes were not illustrated (Gates, *personal communication*). In view of our uncertain knowledge of the morphology of the adult ovary and the shedding of oocytes in *B. bathybates,* the family Biwadrilidae becomes a doubtful candidate for inclusion in the superfamily Lumbricoidea. In many respects it more closely resembles the Criodriloidea not only in the characters of the ovary and the presumed absence of egg-strings but also in the possibly retained primitive character of the anterior situation of the cerebral ganglia in both segments *i* and *ii* and the absence of calciferous glands (structures invariably lacking in aquatic worms). It is however readily distinguishable from both the Criodriloidea and Lumbricoidea by the presence of a supra-oesophageal blood vessel, prostatic glands and a paired lateral line, the latter specialization being indicative of adaptation to an aquatic mode of life. (The only other Oligochaeta known to possess the rudiments of a lateral line are members of the lumbricoid aquatic family Sparganophilidae which further resembles the Biwadrilidae in having the primitive(?) condition of two pairs of latero-parietal vessels and the negative characters of the absence of a sub-neural vessel and spermathecae, the last being of doubtful significance in higher taxonomy.)

It is more likely that the affinities of the Biwadrilidae are revealed by the occurrence of the supra-oesophageal blood vessel, a structure known otherwise only from the mainly southerly occurring Glossoscolecoidea and Megascolecoidea in which the vessel is commonly associated with the extra-mural calciferous glands of terrestrial species. (In *B. bathybates* the vessel, named 'supra-intestinal' by Nagase and Nomura (1937), was described as 'attached directly to the dorsal surface of the alimentary canal, and is distinct in the segements anterior to IX.') It is however, conjectural whether this 'supra-intestinal' vessel in *Biwadrilus* is homologous or even analogous to the supra-oesophageal vessel in the southern earthworms. If homology is accepted, the presence of this blood vessel may not only provide evidence of affinity but possibly that the early forms possessed extra-mural calciferous glands and could have been terrestrial before more recent ancestors became secondarily adapted to an aquatic mode of life. This latter hypothesis however should be viewed with caution for although the aquatic Almidae also lack calciferous glands they too possess a supra-oesophageal vessel. Among other Glossoscolecoidea, the Kynotidae share the same characters but these worms are terrestrial while the Microchaetidae possess calciferous glands yet have no supra-oesophageal vessel.

Any discussion of the origins and antiquity of the group is further compounded by its currently restricted range, Japan, but *see below* Distribution. Presumably the present day Japanese populations are likely to be relicts of a once more widespread group. If the presence of the supra-oesophageal blood vessel is given systematic weighting, the origins would lie in Gondwana where certain of the Glossoscolecoidea and Megascolecoidea also possess this vessel. Possibly the group is of even greater antiquity than either of these two superfamilies and the mosaic of characters could indicate emergence at a time pre-dating the division of Pangaea. In view of the uncertainties surounding the origins and affinities of the family Biwadrilidae, it is prudent to place the family in a separate, monotypic superfamily.

Glossoscolecoidea. The three terrestrial families in this group form a homogeneous assemblage of geographically isolated African and South American earthworms; they differ from the mud-dwelling aquatic Almidae of the tropics of both the New and Old World mainly in the latter's adaptation to an aquatic environment and possessing specializations such as the development of claspers and alae which can evolve only when the restrictions imposed by a soil environment are removed. In addition to the characters of the ovary and the liberation of the oocytes, all four component families possess either or both a supra-oesophageal blood vessel and/or extra-mural calciferous glands. These characters separate them from members of the Criodriloidea and the Lumbricoidea while the absence of prostatic glands with ducts discharging through the male pores or onto adjacent segments, provides a ready means of separating the Glossoscolecoidea except for the Kynotidae, from both the Biwadriloidea and the Megascolecoidea. The origins of this superfamily seemingly lie in the southern hemisphere where members of the Megascolecoidea are dominant. Several fundamental characters are shared with this superfamily: the frequent occurrence of a supra-oesophageal blood vessel and (when present) extra-mural calciferous glands also the subneural blood vessel being free of the nerve cord and adhering to the parietes. Until Gates (1976*a*) recognized the discreteness of the Lumbricoidea, the mutual affinities of the southern families now forming the Glossoscolecoidea were obscured; it is now evident that this superfamily is more closely allied to the Biwadriloidea and the Megascolecoidea than to any other extant groups of earthworms.

Megascolecoidea. In addition to the characters of the ovary and the oocytes forming several egg-strings, members of this superfamily can usually be readily recognized by the male pores occurring by the posterior border of the clitellum, infrequently *xvii,* 17/18 (Eudrilidae), usually *xviii* or rarely *xix* and the presence of prostatic ducts discharging through or nearby to the male pores or onto adjacent segments. The superfamily forms the largest, most diverse and widespread of all earthworm groups. Two families, Ocnerodrilidae and Eudrilidae, are now universally accepted as discrete taxonomic entities but there is disagreement about the diagnostic criteria to be employed to delineate the groups here recognized as the separate families Megascolecidae, Acanthodrilidae and Octochaetidae. (Doubts about ranking have further obscured the fundamental problems confronting taxonomists.) To a large extent these three families are units of convenience, certainly the Acanthodrilidae and the Octochaetidae contain heterogeneous assemblages of genera whose relative distributions reflect the uncertain validities of the families. These apparently anomalous distributions are illustrated by the restrictions of the ranges of genera of the Octochaetidae into two groups, a temperate Australasian component and a tropical assemblage (the latter being largely sympatric with the family Ocnerodrilidae). There have been several attempts at classifying these non-Eudrilid megascolecoids by Omodeo (1958), Lee (1959) and Gates (1959) but the results have not been entirely satisfying while more recent proposals by Jamieson (1971*b*) employ taxonomic criteria which apparently require further investigation (Easton, 1979 : 17). Meanwhile it seems best to retain the (pragmatic) solution contained in the classification proposed by Gates (Sims, 1966). Part of the difficulty in classifying the component genera may be attributed to too few structures being seriously appraised as potential taxonomic characters and, more important, little consideration has apparently been given to the possibility that more than three families may be represented among the currently included genera.

Distribution

Ball (1975) seized on the controversy deriving from rival explanations of Omodeo (1963) and Gates (1929*a* & *b,* 1966, 1967, 1970) concerning the distribution of terrestrial oligochaetes in the northern hemisphere, to illustrate examples of biogeographical hypotheses. In doing so he drew attention to the problems of determining distributions caused by the occurrence of allochthonous species and went on to doubt whether biogeographical studies were possible on earthworms. It is true that such species may cause difficulties to the biogeographer but their importance should not be over-rated (Gates, 1976*b*). Most species of earthworms are highly adapted to their environments and transfer to another habitat can be deleterious causing death, cessation of reproduction or reduction in breeding rates so that new populations fail to become established. However, there are a few species which have wide environmental or feeding tolerances and it these which survive transportation and become established elsewhere. In some instances breeding is favoured as parthenogenesis is more prevalent among allochthonous populations than among autochthonous populations of the same species (Gates, 1956). A few species are spread naturally, i.e. without the intervention of man. The now ubiquitous euryhaline species *Postoscolex corethrurus* (Glossoscolecidae) from northeastern South America is found on or near many tropical and subtropical beaches around the world together with species of *Pontodrilus,* especially *bermudensis,* (Acanthodrilidae) whose origins are unknown, both seemingly are rafted around the tropics. Schwert & Dance (1979) also provided evidence of earthworms being transported by rivers. It is sometimes suggested that cocoons could be carried on the feet of migratory birds but successful transportation by this means seems improbable since cocoons are highly susceptible to desiccation which undoubtedly would occur during extended periods of flight. It is man however, who appears to have been responsible for the transportation of most allochthonous species although the number of species involved represents only a small percentage. Out of a total of some five hundred valid species of perichaetine Megascolecidae, about 15 species are allochthonous while from nearly three hundred species of Lumbricidae only about 10 can also be regarded as allochthonous. Significantly, the most numerous allochthonous Lumbricidae are edaphophagous feeders inhabiting temporary burrows, that is, they are not specialized feeders and are able to withstand disturbance in the soil which they inhabit. These characteristics stand them in good stead and enable them to colonize exotic cultivated soils following the local extinctions of native earthworms (Sims, 1978). Their success comes from their ability to exploit disturbed soils abandoned by native species and not from competing with the latter in their natural (undisturbed) environment.

The terrestrial Oligochaeta are slow-moving animals and being predominantly intolerant of saline conditions, the majority are incapable of bridging marine barriers without the intervention of man which is usually adventitious. They could therefore be regarded as excellent subjects for biogeographical study were it not for the lack of a fossil record. Not only is information on morphology, diversity and frequency of occurrence of ancestral populations no longer available but without fossils, evidence of past distributions has been irretrievably lost too. Without the knowledge of previous ranges, contemporary distributions have a reduced biogeographical significance. The present day absence of a group of earthworms form any area could be due to local extinctions or to the fact that the area had never been populated by their ancestors. Conversely, the presence of a group is equally enigmatic, it could provide evidence of the provenance of origin or merely of a successful recent colonization.

Despite the restrictions preventing valid conclusions being drawn from present day earthworm distributions, for the most part it is still possible to go some way to infer regions of origin. The suborder Lumbricina contains five superfamilies which occur throughout the world except for Antarctica. It may be assumed therefore that ancestral members of the suborder Lumbricina were widespread in the single palaeocontinent of Pangaea which formed at the end of the Palaeozoic from more ancient land masses. It was presumably with the break up of Pangaea and the ensuing isolation which favoured speciation that led to the evolution of the five superfamilies now recognized (and possibly other groups which are now extinct).

Euramerica

The supercontinent of Pangaea began to rift apart in the Triassic with the western extension of the Tethys Sea (Dietz & Holden, 1970) to form the northern continent of Laurasia and the large southern land mass of Gondwana. Subsequent sea-level changes in the north during the Jurassic led to marine incursions which eventually resulted in the formation of two isolated land masses joining by northern land connections what is now eastern North America with Europe and what is now western North America with Asia. The two continents so formed were named Euramerica and Asiamerica respectively (Cox, 1974 : 75). By the late Cretaceous, Euramerica extended from the eastern limits of the Mid-Continental Seaway of

North America to the western shores of the Turgai Straits which separated present day Europe from Asia (Tedford, 1974). The significance of these seas in animal distributions was recognized by Cox (1974) in studies on dinosaurs, Rich (1975) on birds and Platnick (1976) on spiders.

The Lumbricoidea occurs throughout the present day regions which once formed Euramerica. The greatest number of taxa are found in southern Europe, an area which escaped the faunal extinctions which affected the more boreal regions during the Pleistocene glaciations. The family Lumbricidae is not only distributed throughout this vast area but in addition it has spread into China where it is represented by four indigenous species and into Japan where there is a single indigenous species. It seems likely that the five present day indigenous Asian species could be derived from ancestors which successfully colonized parts of the East after the Cainozic closure of the Turgai Straits. The aquatic Sparganophilidae although essentially an Euramerican family, has now been recorded from widely separated localities in the United States but the present day range may have been affected by the development of recent drainage systems. A further complication is that these worms may be spread by man in the roots of water plants as seems likely from the rare records of the family in Britain and France; possibly other New World records, for example from Mexico and Guatemala, may also be due to man's intervention.

The distribution of the family Ailoscolecidae in Euramerica illustrates the affect that plate movements have had on animal distributions. Two genera are known from geologically associated localities in southern Euramerica but subsequent rifting caused members of the family to become widely parted spatially. The genus *Ailoscolex* is now found only in southwestern France while the genus *Komarekiona* inhabits parts of the southeastern United States.

Two other families, Hormogastridae and Lutodrilidae, have ranges consistent with the distribution of the family. The Hormogastridae occurs in countries bordering the western Mediterranean while the Lutodrilidae has been recorded from river or riverside muds in the southeastern United States. In the case of the latter, its present day distributions may differ from its original range since being associated with rivers, individuals may have been carried downstream to colonize new areas as new drainage system developed.

The aquatic monotypic superfamily Criodriloidea is also confined to parts of southern Europe. It occurs therefore in a region where the greatest number of genera and species of its close ally, the Lumbricoidea, have been recorded.

Gondwana

The division of Pangaea in the Triassic not only resulted in the separation of Laurasia from Gondwana but by the close of the era, 180 m.y.a., the latter was split into West Gondwana comprising South America and Africa including Madagascar, the East Gondwana consisting of Antarctica, Australasia and, by then, a detached Peninsular India (Dietz & Holden, 1970). Additionally a single mid-Permian(?) land mass, Pacifica, originating to the east of Australia and Antarctica had split into three groups of fragments; the Kula fragments drifted northwards, the Farallon fragments northeastwards and the Phoenix fragments eastwards (Nur & Ben-Avraham, 1977). By the late Jurassic, 135 m.y.a., the South Atlantic Ocean had begun to open in West Gondwana, a process which continued through to the late Cretaceous, 65 m.y.a. by which time the land connections between western Africa and eastern South America had been severed. Contemporaneously(?) in East Gondwana, the fragments of Pacifica had by then travelled vast distances, the Kula fragments collided with Alaska and eastern Siberia, the Farallon fragments with western North America and the Phoenix fragments with western South America. Although New Zealand had become detached from western Antarctica by the late Cretaceous, the separation of Australia from Antarctica had only just started, a process which continued well into the Oligocene. During this era, peninsular India which had been slowly rifting northwards since the Triassic, was spanning the equator at the fringe of the southwestern limits of the Asian plate (Tedford, 1974); this trek continued until the Neogene when the Indian plate encountered and underthrust the southern margin of Asia, throwing up the Himalayan fold belt by the collision.

The superfamily Megascolecoidea occurs throughout the vast region derived from Gondwana, the family Acanthodrilidae is nowadays the most widely distributed of the group being absent only from tropical South America. The Acanthodrilidae is represented additionally in North America, by *Diplocardia* and *Argilophilus* (a close relative of the Australasian *Plutellus*) but this distribution may be due more to the Farallon fragments transporting ancestors from the southern palaeocontinent of Pacifica to the northeast than to colonization from South America. The possible importance of the transoceanic rifting of fragments of Pacifica to earthworm distributions is seen in the present range of the family Megascolecidae. Although essentially an Australasian group which has spread through the Indo-Australasian archipelago, this family provides the majority of earthworm species in the Kuriles, Japan, Korea and China. It seems more plausible that their ancestors arrived in these areas on the Kula fragments of Pacifica than by any other agency. (A hypothesis which assumes that the family was not once more widely ranging before widespread extinctions occurred.) The present distributions of the more enigmatic and probably artificial family Octochaetidae, may either reflect the spuriousness of recognizing the family taxonomically or merely illustrates the effect of extinctions, for nowadays it comprises temperate species inhabiting Australasia and tropical species occurring in America, Africa and Peninsular India into Burma. The family Ocnerodrilidae is essentially a family of the American and African tropics but interestingly the three genera which form the subfamily Malabarinae, represent the family in peninsular India. If extinctions have not obscured the situation, then presumably the differentiation of the subfamily followed the early rifting of peninsular India from the ancient southern supercontinent. The family Eudrilidae is confined to tropical Africa. Whether the family once had a wider range is problematic but the evidence of numerous genera in western Africa, mostly with limited ranges, leads to a conclusion that the family is currently undergoing a radiation and that it could be newly emergent in the area (*see below* Glossoscolecidae).

The other large superfamily of Gondwana, Glossoscolecoidea, contains four families of which three are soil-dwelling and are found in discrete geographical regions. The family Kynotidae in Madagascar, Microchaetidae in the somewhat arid savannah of southern Africa and the Glossoscolecidae in the forests and mountain grasslands of Central, tropical and subtropical South America. Again if the possibility of extinctions is ignored, then the emergence of these families presumably followed the separation of Madagascar from mainland Africa and the final severance of land links between Africa and South America. It is more probable however that extinctions have occurred. The Amazon basin, for example, provides a rich environment for the Glossoscolecidae yet there are no glossoscolecoid terrestrial worms in the previously adjacent Zaire basin. (Possibly the present radiation of the Eudrilidae in western Africa may be connected with the absence of the Glossoscolecidae or close allies. The Eudrilidae may be seen to be actively exploiting niches left vacant after the extinction of terrestrial glossocolecoids whose disappearance may well have been hastened or caused by this more successful family or by environmental factors, for example, the marine incursions in the area during the Cretaceous (Fig. 2).

A further example of the probability of extinctions having occurred to affect the present range of the superfamily is seen in the present relict distribution of the Microchaetidae within South Africa. The pampas at comparable latitudes in South America contains no glossoscolecoids yet the environment is not entirely dissimilar to the South African veld, a habitat which itself has become reduced within historical times (Sims, 1978 : 672). The fourth family comprising the Glossoscolecoidea is the predominantly aquatic Almidae which, unlike other members of this superfamily, is widely distributed. The Almidae occurs throughout the muds of rivers and lakes in the tropics of the Americas, Africa, peninsular India and parts of southeast Asia being mainly sympatric with the megascolecoid Ocnerodrilidae and tropical Octochaetidae. Presumably its emergence, like those of the two megascolecoid families, pre-dated the division of southern India from the Gondwana

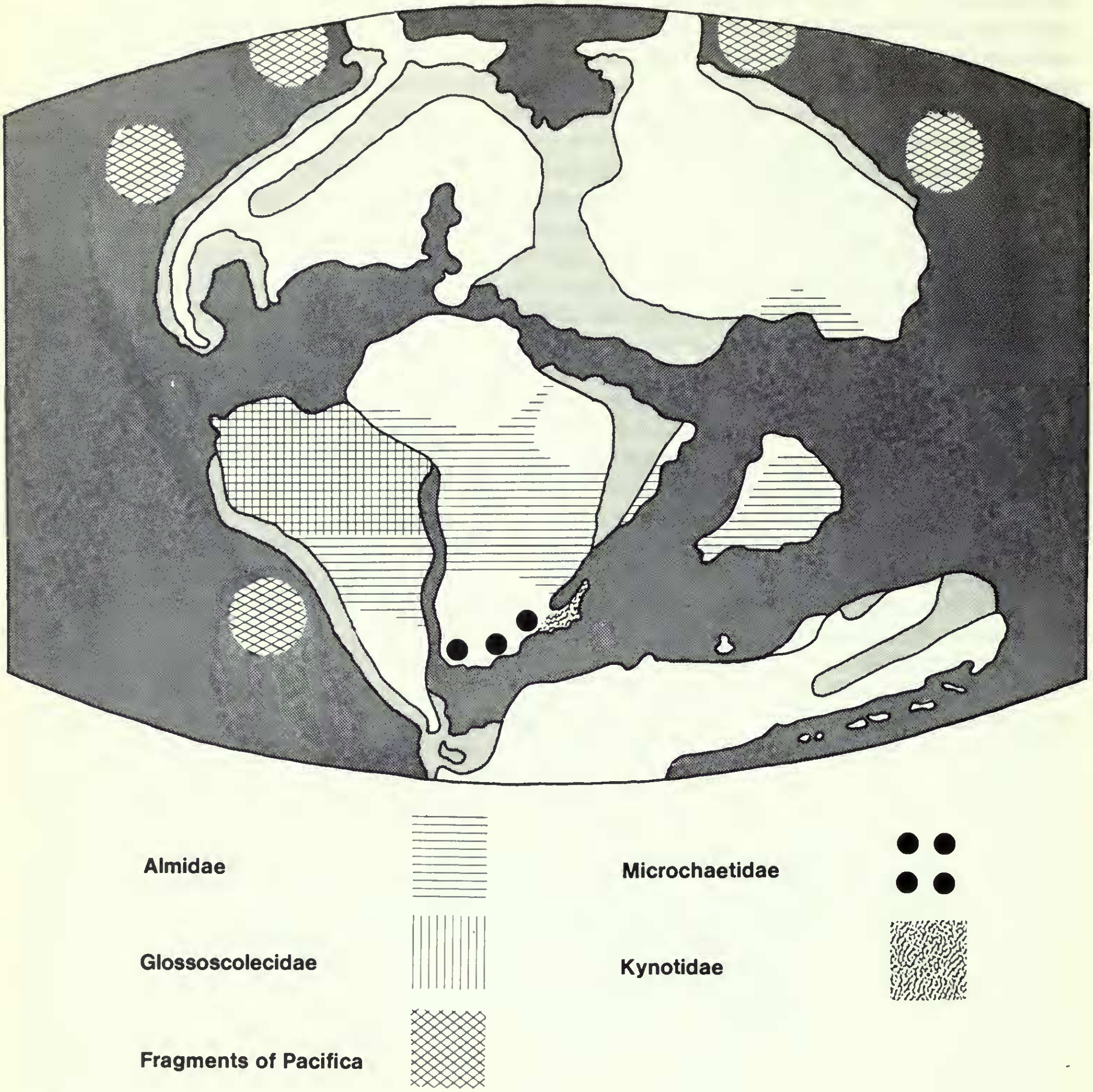

Fig. 1 The distribution of land and sea at the end of the Jurassic 135 m.y.; a reconstruction of the continents with continental shelf and epicontinental seas after Tedford (1974); the locations of fragments of Pacifica superimposed according to Nur & Ben-Avraham (1977). The *present day* distributions of members of the superfamily Glossoscolecoidea are shown on the land areas.

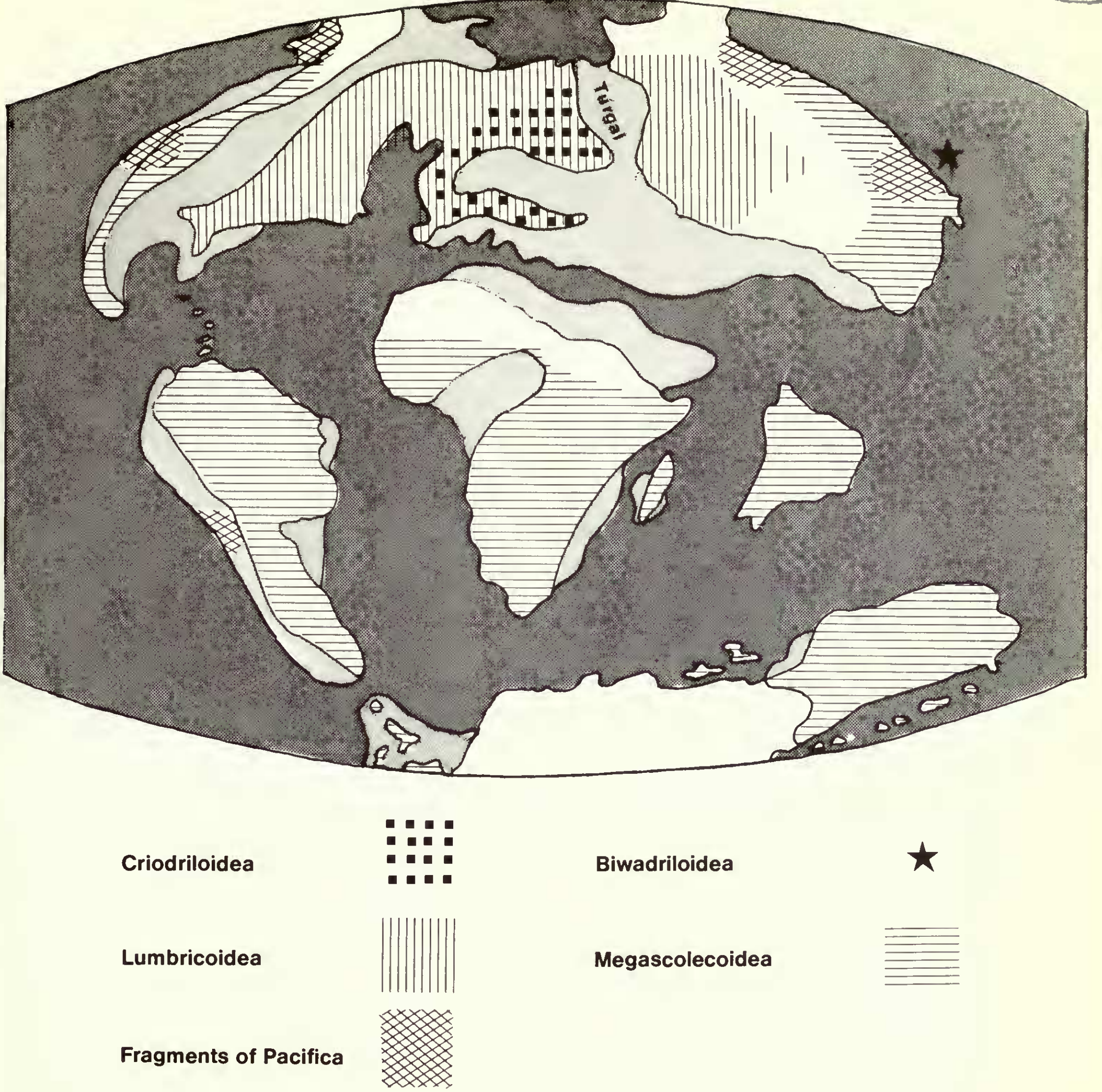

Fig. 2 The distribution of land and sea at the end of the Cretaceous 65 m.y.: a reconstruction of the continents with a continental shelf and epicontinental seas after Tedford (1974); the locations of fragments of Pacifica superimposed according to Nur & Ben-Avraham (1977). The *present day* distributions of members of the suborder Lumbricina other than the subfamily Glossoscole-coidea, are shown on the land areas.

Erratum. This page replaces 121 in *Bull. Br. Mus. Nat. Hist.* (Zool.) **39**(2): 103–124.

mainland and the opening of the southern Atlantic Ocean. The family Almidae also extends from Asia along the Indo-Australasian archipelago as far as Sulawesi. This distribution may provide evidence that formerly the family and superfamily were widespread throughout the whole of Gondwana including Australasia but subsequently extinctions occurred in the east. Alternatively, the eastward extension of range from India could have been effected during the Oligocene when peninsular India passed close by southeast Asia during its stately progress northwards. After first invading the Asian plate, opportunity for further colonizations occurred during subsequent sea-level fluctuations, for example during the Miocene and early Pleistocene when at times the South China Sea was no more than a river valley (Fitch, 1954).

The smallest superfamily is the monotypic Biwadriloidea whose single species is now confined to rivers and lakes in Japan. On its morphology, this worm shows a close affinity with the austral Megascolecoidea and Glossoscolecoidea; it would seem therefore to be a relict of stock derived from Gondwana. If this conclusion is correct then it may be postulated that its ancestors populated the mid-Permian portion of Gondwana, Pacifica, which eventually split into several pieces. These worms, like some Megascolecoidea, were transported at least by the Kula fragments now located in eastern Siberia and Alaska. As mentioned above, the possibility that this group emerged before the late Palaeozoic break-up of Pangaea cannot be excluded.

Postscript and Acknowledgement

Studies on the classification of earthworms reported here originated partly from a long held personal dissatisfaction with Lumbricine systematics but more immediately to meet a publisher's requirement to provide a diagnosis for each category of the megadriles from subfamily upwards. The latter request was so reasonable that it was incumbent on me to accede but with the knowledge that a re-appraisal of the classification of the Lumbricina could not be delayed further. The most promising contribution on this topic had already been made by the doyen of oligochaetology, Dr G. E. Gates in his (1976*a*) paper on the Lumbricoidea, 'On earthworm ovaries and their importance in megadrile systematics. I'. Accordingly a preliminary survey was made of the Lumbricina centred on the group of characters which Gates had employed to define the Lumbricoidea. Then correspondence with Dr Gates elicited the information that because of ill-health and advancing years, Part II of his planned series of papers on the systematic importance of earthworm ovaries would never be published; however as our general conclusions were in agreement, he generously provided a digest of relevant observations and his opinions on megadrile classification for whatever use could be made of them. The present paper therefore owes much to the co-operation and goodwill of Dr Gates to whom I am deeply grateful for so willingly relaying his views to me. Nevertheless, as in any healthy, fruitful discussion we did not agree on all matters, so in several details I am claiming an author's prerogative and have expressed my own views; of these I absolve Dr Gates from responsibility should they be found wanting.

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